Spatial and Temporal Variability in Zooplankton Abundance of the Great Lakes

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SPATIAL AND TEMPORAL VARIABILITY IN ZOOPLANKTON ABUNDANCE OF THE GREAT LAKES

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ABSTRACT

Minns, C. K. 1984. Spatial and temporal variability in zooplankton abundance of the Great Lakes. Can. MS Rep. Fish. Aquat. Sci., 1750.

Data from several surveys of zooplankton distribution and abundance in the Great Lakes are summarized to give total biomass, and cladoceran, calanoid, and cyclopoid abundance. The summaries by station and cruise are analyzed to examine the relative importance of, and significance of spatial and temporal variability. The results are assessed and their relevance to the design of future zooplankton studies examined.

RESUME

Minns, C. K. 1984. Spatial and temporal variability in zooplankton abundance of the Great Lakes. Can. MS Rep. Fish. Aquat. Sci., 1750.

On a fait des résumés des données de plusieurs études de la distribution et de l'abondance du zooplancton dans les Grands Lacs pour obtenir la biomasse total et l'abondance des cladocéres, calanoïdes et cyclopoïdes. On analyse les résumés par station et par sortie pour examiner l'importance relative et la signification de la variabilité spatiale et temporelle. On évalue les résultats et on étudie leur pertinence pour les futures études sur le zooplancton.

INTRODUCTION

Limnological surveys of large lakes are generally limited to sampling many locations on few occasions. This follows the practices of oceanography. Until recently, statistical tools for separating temporal and spatial effects were largely unavailable or underdeveloped, but those analyses that were available together with evidence from small-scale studies, indicated that much more useful information, both scientific and managerial, would be obtained by sampling few locations on many occasions. The purpose of this study was to assess the relative importance of spatial and temporal variability in zooplankton abundance ($n\ m^{-3}$) as determined by large-scale surveys on most of the Great Lakes, and to use the results to recommend preferred designs for future zooplankton surveys.

From 1970 to 1974, the Great Lakes Biolimnology Laboratory undertook extensive surveys to determine the distribution and abundance of zooplankton in the International Great Lakes. Detailed analyses of the studies on the various lakes have been reported by Watson & Carpenter, 1974; Watson, 1974; Watson & Wilson, 1978, etc. The data from these surveys were summarized for analysis to give cladoceran, cyclopoid, calanoid, and total abundance by cruise and station. A statistical model, described by El-Shaarawi & Shaw (1978) and used by El-Shaarawi & Kwiatkowski (1977), was used to examine the temporal and spatial variability.

MATERIALS AND METHODS

The zooplankton sampling and enumeration procedures used on the zooplankton surveys have been described by Watson and Carpenter (1974). For the analysis, stations which had been visited less than three times

were eliminated.

El-Shaarawi and Kwiatkowski (1977) described an analysis of variance procedure whereby the contributions of spatial (station) and temporal (cruise) variance are assessed. The ANOVA model used is as follows:

$$F(Z_{ij}) = \mu + \alpha_i + \beta_j$$

where α_i's and β_j's are cruise and station coefficients. Least square is used to estimate μ, α's, β's and θ^2, the variance. All data were transformed to meet the criteria of ANOVA using the generalized transformation:

$$Z_{ij} = \frac{Y\lambda_{ij} - 1}{\lambda}, \quad \lambda \neq 0$$

$$\log_e Y_{ij}, = 0$$

where λ is an unknown constant and Y_{ij} is an observation from the i-th cruise and j-th station. Maximum likelihood is used to select λ.

El-Shaarawi and Shaw (1978) described an elaboration of the ANOVA whereby, subsequent to the analysis, the data can be classified into spatial zones using a hierarchical iterative procedure. The grouping process is limited by preselecting levels of discriminant significance.

RESULTS

The results of the ANOVA show that in all cases temporal variability was of greater significance than spatial (Table 1). Comparison among the groups and with the total, show that cladoceran abundance was the predominant factor. While most of the F ratios were significant at $P < 0.001$, some station F ratios were only significant at higher probabilities or not at all, as in the cases of the calanoids of Lake Ontario in 1970 and the cyclopoids of Lake Erie in 1970. Quantitatively, these results are similar to those obtained for temperature and nutrients in Lake Ontario (El-Shaarawi

and Kwiatkowski, 1977), phytoplankton abundance in Lake Superior (El-Shaarawi and Shaw, 1978) and temperature and nutrients in the Upper Great Lakes (Kwiatkowski, 1980).

As an additional comparison, the ratio of station to cruise variance was calculated as an index of importance (Table 1), following the example of Lewis (1978). When compared to Lake Erie and Ontario, the ratios for total, cyclopoid, and calanoid abundance are higher in the Upper Great Lakes, but the ratios for cladocerans do not vary as much or in the same pattern.

The seasonal trends from cruise to cruise, as reflected by the estimated α_i's conform to an expected pattern in all lakes (Fig. 1). In general, the cladocerans show the most pronounced seasonal variation with abundance increasing in the summer.

Spatial zones were defined, although they were of less significance than the temporal trends. Significance levels were selected to show two or more zones (Table 2), rather than to demonstrate statistical discrimination at a low probability level. The latter would usually only result in the separation of one or two stations from the rest. The zones typically show (Fig. 2) an inshore-offshore gradient with pronounced 'highs' in areas already noted for their stressed condition, eg. Duluth, Saginaw Bay, western Lake Erie.

DISCUSSION

These results for the Great Lakes zooplankton community show that temporal variation is many times more significant than spatial variation. There are spatial patterns, but the loosely demarcated 'zones' appear to result from the outward mixing of an altered or stimulated community at the

edge (shoreline) with an underlying uniform open-lake community. At the shoreline where most stresses are greatest, plume-like patterns are seen, which often spread along the shore in a counter-clockwise direction consistent with the general rotation in the lakes. The origin of these plumes are easily identified with familiar centres of pollution. Lewis (1978) describes such patterns as 'fixed spatial gradients'. The ratios of spatial to temporal variance are higher for total cyclopoidal and calanoid abundance in the Upper than Lower Great Lakes and may be attributed to two factors. First, in the oligotrophic Upper Lakes, the disparity between open lake and inshore stressed areas is greater than in the Lower Lakes. Second, cladocerans are generally less important in the Upper Lakes and thus the total ANOVAs on total abundance are less affected.

The temporal F ratios for cladocerans are generally higher than those for the other two groups because of differences in life histories. Cladocerans have short life-spans and follow a seasonal boom-bust population cycle, while copepods, which have much longer life spans, show greater temporal stability and continuity.

Consideration of these results, particularly the spatial aspects, must be tempered by the realization that they are derived from unreplicated sampling. There is a great underlying variability. Hubschman (1960) found that cladoceran abundance at a single station in Lake Erie varied by as much as five times on successive days. Torke (1975) and J. B. Wilson (pers. conv.) have noted similar, though less severe problems with replicated sampling. The cruises in the zooplankton surveys studied here are usually several weeks apart. Thus, it is likely that spatial discrimination would only be possible at the extreme, e.g. Saginaw Bay vs.

central Lake Huron, if replicates had been taken. Further, the lack of replication prevents an examination of the variance component due to temporal-spatial interactions which must be present. Theriault and Platt (1978), in a study of phytoplankton biomass in St. Margarets Bay, Nova Scotia, found that temporal variation was of far greater significance than spatial. They also found that there was a space/time interaction which was greater than the spatial component.

Rastonis et al. (1978) have offered a framework for monitoring where objectives are linked to sampling and duration requirements. They give quite specific targets with respect to frequency of sampling; frequency should be related to the rates of change in the observed. Spatial resolution is only loosely defined, although categories such as 'open lake', 'tributary mouths' and 'areas of restricted circulation (harbours, bays, etc.)', are identified. Zooplankton abundance can change rapidly, thereby greatly affecting the abundance of algae, and can be greatly affected by the predation of fish. For instance, Hawkins and Evans (1979) studied the seasonal variation of zooplankton abundance in a nearshore area of southeastern Lake Michigan over three years. They sampled by month and found that while overall seasonal patterns of abundance were consistent from year to year, the peak timing for cladocerans and copepods was variable. They also concluded that monthly sampling was inadequate for following cladoceran fluctuations. Torke (1975) showed that temporal abundance variations and life histories of zooplankton species at a deep-water station in Lake Michigan could be followed with weekly sampling. Selgeby (1975) was able to follow the life history patterns of most species with bi-weekly sampling in the outlet of Lake Superior.

Thus, the strength of these surveys lay in the general description of the seasonal cycles of abundance. Spatially, they can only discriminate the extremes of the gradients that were present, being only intended to describe the then unknown temporal and spatial variability. As it turned out, the station numbers were greater than necessary to cover the spatial variation and the frequency was too low to allow a detailed study of the abundance and community dynamics. The spatial variations, though weak, are present primarily at the shoreline, in the bays, and near the main tributary inputs. The extensive surveys gave too great attention to the main open-lake areas where there is little spatial variation. The important areas of perturbation are well known, but in these surveys they were only represented by a few stations.

CONCLUSION

Clearly, monitoring programs for biological communities such as zooplankton must emphasize the study of temporal variation. Spatial discrimination should be limited to a few points along the 'fixed station gradient'. For instance, Lake Erie zooplankton might be adequately monitored using three stations, one in each basin. This is to say that the Great Lakes should be treated more like lakes and less like oceans when monitoring programs are designed. Adoption of oceanographic approaches was acceptable for preliminary description of the Great Lakes, but the continued use of 'lake-wide means concentration' and such like for monitoring was inappropriate.

Perturbations, both natural and man-made, produce changes in biota. These changes come about as a result of altered growth and reproductive and mortality rates, which can only be determined adequately with high

frequency sampling. Only finite resources are allocated for monitoring purposes and they must be used to the greatest effect if lake responses to management are to be correctly interpreted.

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Fig. 1 Seasonal trends in cruise coefficients (α_i's) for zooplankton in the Great Lakes (Ontario 1970, Erie 1970, Huron 1971, and Georgian Bay 1974,--right hand scale for calanoids (□). North Channel 1974,--left hand scale for cladocerans (o)).

Fig. 2 Spatial zones of zooplankton abundance in the Great Lakes.

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Table 1. CRUISE AND STATION VARIANCE RATIOS FOR GREAT LAKES ZOOPLANKTON[1,2]

Lake	Year	Degrees of Freedom			Cladocerans			Cyclopoids			Calanoids			Total		
		Cruises	Stations	Residuals	Fc	Fs	Ss:Sc[3]	Fc	Fs	Ss:Sc	Fc	Fs	Ss:Sc	Fc	Fs	Ss:Sc
Lake Ontario	1970	12	32	331	91.85	4.47	0.130	49.18	1.79**	0.097	11.53	1.49*	0.345	66.72	1.95***	0.078
Lake Ontario	1972-3	8	31	225	166.04	6.44	0.150	52.25	2.49	0.185	27.08	1.12--	0.160	66.26	2.57	0.150
Lake Erie	1970	9	29	246	26.59	2.67	0.324	49.72	1.29-	0.084	19.17	1.73*	0.291	43.22	2.59	0.193
Lake Huron	1971	7	32	189	80.83	6.34	0.359	25.19	3.27	0.593	25.32	1.85**	0.334	44.16	5.23	0.541
Georgian Bay	1974	6	34	191	95.49	4.74	0.281	25.37	4.30	0.960	15.33	3.09	1.142	32.71	5.01	0.868
North Channel	1974	6	12	53	50.06	4.05	0.161	13.82	4.16	0.602	7.58	2.83***	0.747	15.93	3.61	0.453
Lake Superior	1973	5	82	366	246.51	5.58	0.371	23.41	5.59	3.916	49.17	2.11	0.704	35.81	3.47	1.589

1: All F statistics significant at $P < 0.001$ except:- ***, $P < 0.005$; **, $P < 0.01$; *, $P < 0.05$; -, $P > 0.1$; --, $P > 0.2$

2: All data transformed using $\lambda = 0$ except for

$\lambda = 0.5$ - Ont. 70 cal; Erie 70 cal; Huron 71 cal; North Channel 74 cyc, cal, tot.(cal = calanoids, cyc = cyclopoids, tot = total)

$\lambda = -0.5$ - Georgian Bay tot.

3: Ss:Sc - Ratio of station variance to cruise variance.

Table 2. SIGNIFICANCE LEVELS FOR 'ZONE' DEMARCATION

Lake	Year	Cladocerans	Cyclopoids	Calanoids	Total
Lake Ontario	1970	0.20	0.10	0.20	0.20
Lake Ontario	1972-3	0.10	0.20	0.20	0.20
Lake Erie	1970	0.20	0.20	0.20	0.20
Lake Huron	1971	0.10	0.10	0.20	0.05
Georgian Bay	1974	0.05	0.10	0.20	0.05
North Channel	1974	0.05	0.05	0.20	0.05
Lake Superior	1973	0.10	0.05	0.20	0.10

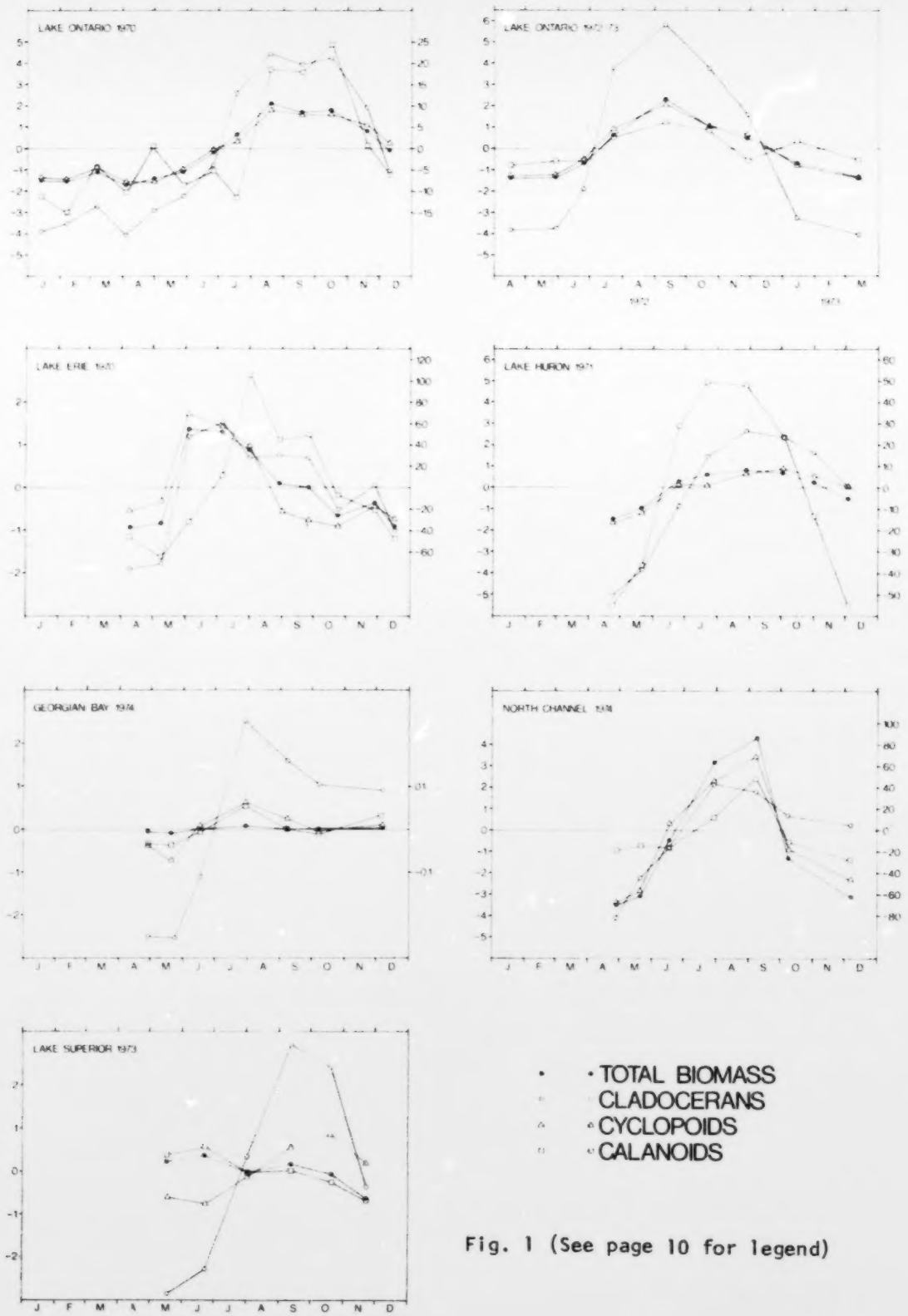

Fig. 1 (See page 10 for legend)

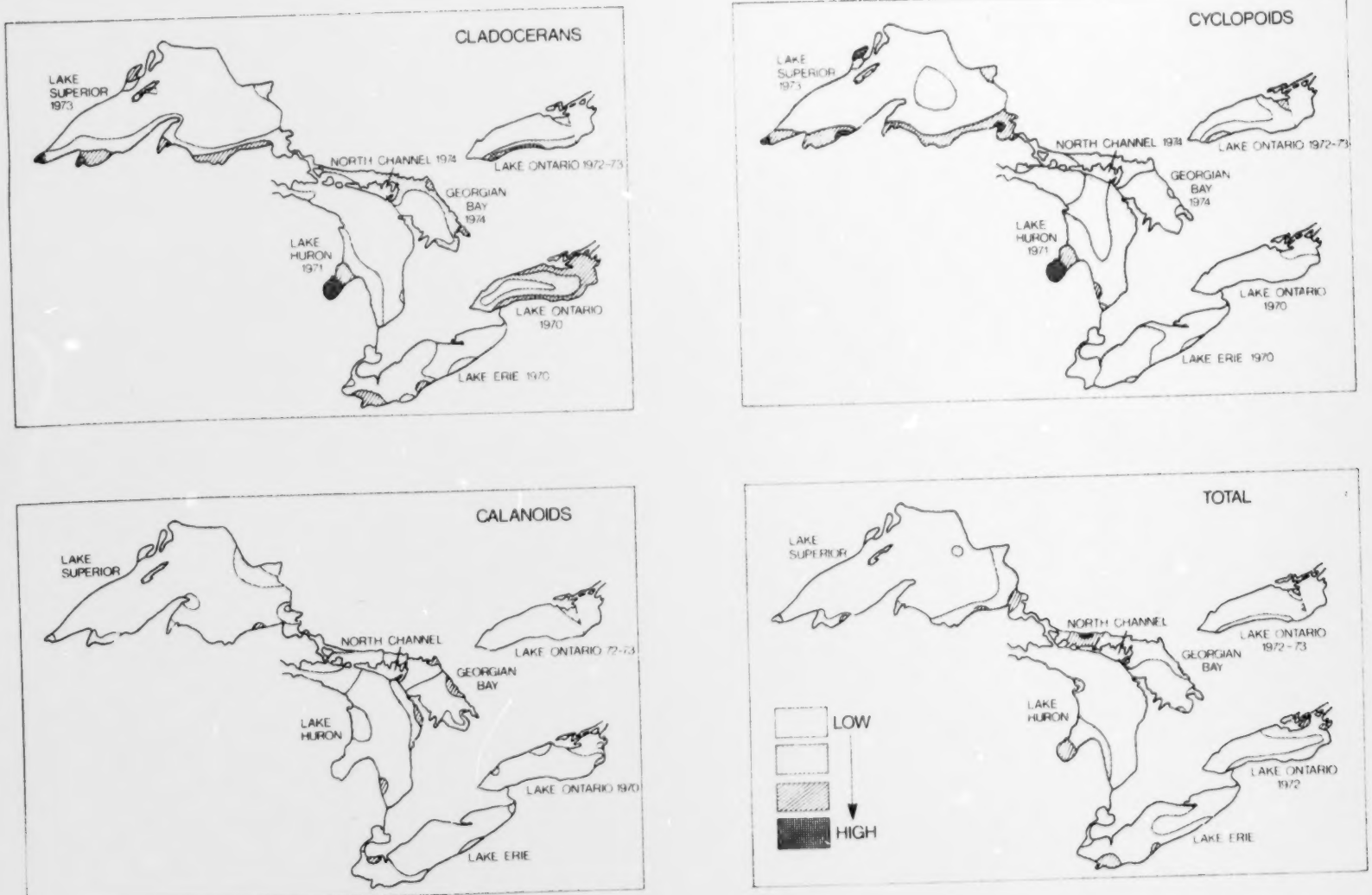

Fig. 2 Spatial zones of zooplankton abundance in the Great Lakes